Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over *Vaccinium* shrubs in the field layer

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ABSTRACT

The moose (*Alces alces*) is a dominant large mammalian herbivore in the world's boreal zones. Moose exert significant browsing impacts on forest vegetation and are therefore often at the centre of wildlife-forestry conflicts. Consequently, understanding the drivers of their foraging behaviour is crucial for mitigating such conflicts. Management of moose in large parts of its range currently largely ignores the fact that moose foraging is influenced by increasing populations of sympatric deer species. In such multispecies systems, resource partitioning may be driven by foraging height and bite size. Feeding competition with smaller species might replace larger species from the field layer and drive them towards higher foraging strata offering larger bites. This bite size hypothesis has been well documented for African ungulate communities. Based on a large diet DNA metabarcoding dataset we suggest that feeding competition from three smaller deer species (red deer *Cervus elaphus*, fallow deer *Dama dama*, and roe deer *Capreolus capreolus*) over *Vaccinium* shrubs in the forest field layer might drive moose towards increasing consumption of Scots pine (*Pinus sylvestris*) in Sweden. We found that in areas of high deer density, moose diets consistently contained less *Vaccinium* and higher proportions of pine over three spring periods. Utilization of these food items by the smaller deer species was either unaffected by deer density or, for *Vaccinium* showed the opposite pattern to moose, i.e., increases of proportions in the diet of roe and red deer with increasing deer density. Availability of pine and *Vaccinium*, measured as proportion of available bites, did not explain the observed patterns. Our results suggest that managing key food items like *Vaccinium* and the populations of smaller deer may play an important role in controlling browsing impacts of moose on pine.

1. Introduction

The moose (*Alces alces*) is a dominant large mammalian herbivore across the world's boreal zone and a major driver of the functioning of boreal forests (Pastor et al., 1988). Moose are also the central player in human-wildlife interactions in these areas, being a highly valued game species across North America and Eurasia but also a concern for forestry due to their impacts on commercially exploited tree species (Horne and Petäjistö, 2003, Ezebilo et al., 2012, Herfindal et al., 2015, Timmermann and Arthur, 2017). Moose management across the boreal zone thus focuses on both these goals; maintaining healthy, harvestable, populations of moose while minimizing moose-forestry conflicts (Timmermann and Arthur, 2017, Dressel et al., 2018, Schrempp et al., 2019). During the last three decades, the ranges of smaller deer species, such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in Europe and white-tailed deer (*Odocoileus virginianus*) in North America have been expanding and their numbers increasing (Côté et al., 2004, Linnell et al., 2020). As a result, North American and Eurasian
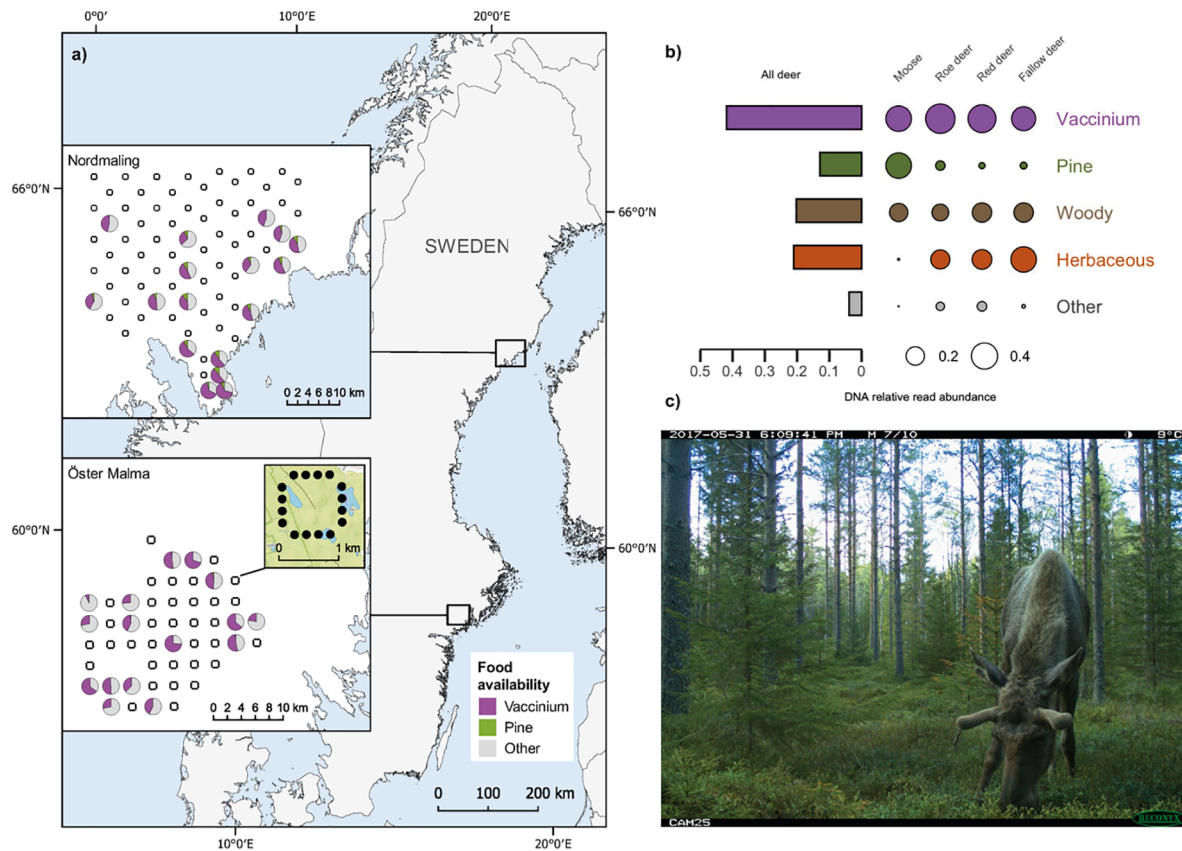

Fig. 1. (a) Location of the study regions in Sweden and sampling grids of square transects (large insets). The small inset shows the layout of 16 sampling plots for pellet group counts within each square transect. The subset of 33 transects on which food availability was measured in addition to deer density is indicated by pie charts showing food availability. (b) Composition of spring diets at the community level (all deer) and for the individual deer species (moose *Alces alces*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, and fallow deer *Dama dama*). The length of bars and size of circles corresponds to the average proportions of food items. 'Woody' refers to all woody plants other than pine or *Vaccinium*. (c) Bull moose feeding on *Vaccinium* in the Nordmaling study region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

moose have increasingly faced the challenge of coexistence with smaller deer species (Schmitz and Nudds, 1994, Linnell et al., 2020). Given the large potential diet overlap among these deer species (Spitzer et al., 2020), we expect the smaller deer to strongly influence moose resource use and, thus, ultimately the impacts of moose on forests and forestry. Here, we investigate these largely unexplored relations, using Swedish moose and multispecies ungulate communities as our model system (Linnell et al., 2020).

The mechanisms that shape sympatric coexistence among species are complex, but a few unifying hypotheses exist. Under circumstances of competition, natural selection favours the separation of ecologically similar species (Pianka, 1988). Such separation can be achieved through resource partitioning on a spatiotemporal scale and, for ungulates, through diet partitioning, which has been widely cited as a key mechanism facilitating their coexistence (Putman, 1996, Kirchhoff and Larsen, 1998, Mysterud, 2000, Bertolino et al., 2009, Azorit et al., 2012, Obidzinski et al., 2013).

Much research attention has been directed towards understanding partitioning in grazing systems (Bell, 1971, Illius and Gordon, 1987, Arsenault and Owen-Smith, 2002) whereas the mechanisms driving partitioning in browsing guilds remain less understood. A standard explanation is that browsers use differences in body size to feed at different heights in the vegetation (McNaughton and Georgiadis, 1986). Empirical testing of this 'feeding height hypothesis' has shown that such stratification indeed exists. For example, Nichols et al. (2015) found browsing heights for moose to be significantly higher than those of smaller deer, and Cameron and du Toit (2007) suggested that giraffe (*Giraffa camelopardalis*) were 'winning by a neck' through avoiding competition in a feeding guild with shorter browsers. The same studies, however, also reported substantial interspecific overlap in browsing height. These findings suggest that resource partitioning might actually be driven by the smaller foragers. According to Woolnough and du Toit (2001), who studied African browsing guilds, the mechanism through which smaller browsers push larger species to browse upwards is bite size. Herbivores are faced with the challenge that plant foliage is of poor nutritional value, which necessitates bulk intake and turns eating time and digestion into important constraints (Owen-Smith and Novellie, 1982). Because large bites allow for more food intake per unit time than smaller bites (Spalinger and Hobbs, 1992), bite size rather than plant biomass may regulate intake rates among browsers (Spalinger et al., 1988). On the other hand, digestible energy concentration in woody browse declines as stem diameters increase (Shipley and Spalinger, 1995) and the higher fibre content of large stems also requires longer digestion time (Demment and Van Soest, 1985, Shipley et al., 1999). Since larger herbivores can tolerate lower quality, high-fibre diets than smaller species (Müller et al., 2013), foraging strata offering large bites may offer large herbivores access to resources that are not available to smaller browsers (Shipley, 2007). Cameron and du Toit (2007) showed that giraffes gained an advantage through browsing above the reach of smaller competitors, enabling them to take larger bites that yielded more biomass per bite than bites in the lower strata. A similar mechanism might exist for moose, the largest browser in the northern hemisphere. Shipley et al. (1998) reported that foraging moose ignored over 50% of available browse and chose browse species offering fewer larger stems over those with many smaller stems, thus prioritizing intake rate.

In boreal forests, there are two main foraging strata for browsing ungulates; the field layer (from the ground to a height of ca. 50 cm), often dominated by ericaceous shrubs, and the understory above the field layer consisting of immature coniferous and deciduous trees, such as pine, spruce, and birch species that are shorter than the main canopy. *Vaccinium* dwarf shrubs growing in the field layer are important staple food sources throughout the year for all deer species in the boreal zone; as has been described for moose (Cederlund et al., 1980, Hjeljord et al., 1990, Saether et al., 1996, Wam et al., 2010, Schrempp et al., 2019), roe and red deer (Mysterud et al., 1997, Mysterud, 2000, Barancekova et al., 2010, Krojerova-Prokesova et al., 2010), and fallow deer (Obidzinski

et al., 2013). Within the tree sapling layer, Scots pine (*Pinus sylvestris*) is the dominant food item for Scandinavian moose, frequently comprising 50% or more of their diets during winter and early spring (Cederlund et al., 1980, Shipley et al., 1998). Because pine is also one of the economically most important timber species in Sweden, browsing damage by moose is the main cause for the moose–forestry conflict. Countrywide, approximately 17% of young pine stems are affected by browsing damage (Pfeffer et al., 2021). The economic cost of wildlife damage to the Swedish forest sector has been estimated as 7.2 billion Swedish crowns (ca. 831 million USD) annually (Bergquist et al., 2019). Because *Vaccinium* shrubs form a large part of the diets of all four deer species (Cederlund et al., 1980, Mysterud et al., 1997, Barancekova et al., 2010, Krojerova-Prokesova et al., 2010, Obidzinski et al., 2013), whereas pine is mostly consumed by moose alone (Cederlund et al., 1980, Nichols and Spong, 2014, Spitzer, 2019), we expected that any shifts in resource use resulting from competition with the smaller deer would be most apparent between these food items. Moreover, similar to the African situation, bite size varies across the layers and is generally larger in the tree sapling than in the field layer stratum. Pine, in particular, may provide large bite sizes relative to the *Vaccinium* dwarf shrubs. The two most common *Vaccinium* species in Sweden, bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea*) bear small leaves on a condensed framework of thin stems (ramets) whereas Scots pine offers long, paired needles which are densely packed on thicker stems. Additionally, the use of the field layer by abundant populations of smaller deer may strongly reduce the height of the *Vaccinium* shrub layer and likely further reduce bite size (Baines et al., 1994, Hegland et al., 2005).

Based on these assumptions, we investigated the idea that feeding competition from smaller deer over shrubs in the field layer drives moose towards increasing consumption of pine. In our study system, we expected feeding competition to manifest as a form of resource competition where feeding exploitation of shrubs modifies the latter in such a way that it leads to a competitive displacement of moose. In areas of high deer density, the availability of shrubs, or at least bulky bites of shrubs, would be suppressed by deer and the 'feeding height' and 'bite size' hypotheses predict that moose would then switch to the higher stratum of pine trees, which also offers larger bites. Under such conditions, growing numbers of smaller deer could therefore exacerbate the moose-forestry conflict. We tested this prediction using a strong population density gradient of the three aforementioned deer species (hereafter referred to as 'deer density') to investigate whether their presence elicits a change in the foraging patterns of moose during early spring. This season marks the period when the supply and choices of forage are limited and partitioning of shared resources should be most apparent. To quantify the resource use patterns of moose and the smaller deer in order to test our hypothesis, we used a large diet DNA metabarcoding data set (Taberlet et al., 2007, Valentini et al., 2009, Taberlet et al., 2018).

2. Material and methods

2.1. Study area

The study area included two regions in Sweden; a region in northern Sweden close to the town of Nordmaling and a region in southern Sweden near Öster Malma (Fig. 1a). A mosaic of boreal forests, mires and agricultural land characterizes both regions. Common tree species include Scots pine, Norway spruce (*Picea abies*), birches (*Betula* spp.), poplars (*Populus* spp.), and willows (*Salix* spp.). Ericaceous shrubs (particularly of the genera *Vaccinium*, *Calluna*, and *Empetrum*), mosses and lichens dominate the field layer. Agriculture comprises a mixture of small to medium scale pastoral and arable farms, with cereals, root vegetables or fodder being common crops and is more dominant in the southern region. Moose, roe deer, red deer, and fallow deer occur sympatrically in both regions. Wild boar (*Sus scrofa*) also occurs but is currently restricted to Öster Malma, and reindeer (*Rangifer tarandus*)

sporadically appear in Nordmaling during the winter. In each region, we used sampling grids of 1x1 km square transects (76 in Nordmaling and 50 in Öster Malma) spaced on average 3–6 km apart, which were established as part of a long-term environmental monitoring program (FOMA, 'Fortlöpande miljöanalys', Edenius (2012)) and the Beyond Moose research program (Pfeffer et al., 2018).

2.2. Sample collection

We collected fresh fecal samples of moose, red deer, fallow deer and roe deer for diet analyses through DNA metabarcoding along the whole length of each square transect (4 km). On all 126 transects, we collected samples during spring (March-April in Öster Malma and April-June in Nordmaling) every year from 2015 to 2017 as part of annual pellet group counts. These samples thus reflect spring diets as they were collected just after snowmelt, which on some of the northernmost transects extended into late May to early June. Additionally, to assess seasonal diet variation, we collected samples on a subset of 33 transects on a bimonthly basis from September 2016 to November 2017. For practical reasons, we sampled half the 33 transects alternatingly each month. For both the annual spring sampling and the bimonthly sampling during 2016–2017, we aimed at collecting five samples for each deer species per transect and visit, placing at least 200 m between samples from the same putative species to maximize the chance of sampling different individuals. For determination of ungulate species and diet composition through DNA analysis, we placed approximately 2 g of fresh ungulate feces into sterile, airtight 20 mL scintillation tubes filled with silica gel desiccant (~1–3 mm, with indicator [orange gel], Merck KGaA, Germany) (DeMay et al., 2013, Taberlet et al., 2018). Fecal samples were considered fresh if they still had a shiny, wet surface and were free from signs of infestation by coprophages (Hemami and Dolman, 2005). To prevent contamination, we used disposable plastic spoons or nudged pellets directly into the tubes, avoiding all contact with other samples or the collector. The silica-dried samples were then stored at room temperature in the dark until further processing.

2.3. DNA metabarcoding and diet data set

We chose DNA metabarcoding over alternative methods such as microhistology as it offered the possibility to determine both deer species and the diet composition from the same fecal sample. Without DNA verification, misclassification of fecal pellets from similarly sized deer species can be a serious problem (Spitzer et al., 2019). Moreover, DNA metabarcoding does not depend on observer experience, requires less time in case of large sample sizes, and can be directly compared with results of other DNA metabarcoding studies as long as the same markers and protocols are being used. However, like many new technological advances in science, DNA metabarcoding is not free from challenges. These include marker limitations (Taberlet et al., 2007) and PCR amplification bias (Pawluczyk et al., 2015, Nichols et al., 2018), which can affect the quantities of sequence reads and lead to under- or over-estimations of diet components. In case of herbivore diets, the quantity and quality of DNA in fecal samples may also be affected by differences in digestibility or variation in chlorophyll concentrations across plant species and tissues. By using standardized methods across DNA meta-barcoding experiments and ecological treatments or gradients, as we did in our study, such biases can be expected to be consistent across those treatments or gradients. Relative differences in diet compositions should therefore constitute true ecological signals that reflect actual changes in consumption even if the proportions consumed and the proportions detected may not be an exact match. Despite these caveats, diet

quantification with DNA metabarcoding is not worse than other methods (Taberlet et al., 2018) and has been shown to yield similar result to alternative methods such as isotopic proportions (Kartzinel et al., 2015) or microhistology (Nichols et al., 2016). All fecal samples included in this study were processed according to the same DNA extraction and metabarcoding protocols.

DNA extraction and purification were carried-out on a QIASymphony SP platform using the DSP DNA minikit (Quiagen, Hilden, Germany) according to the manufacturer's instructions.

To confirm deer species, we followed protocols of Spitzer et al. (2019) and amplified a section of the mitochondrial 16S gene for identification of mammalian species (primers MamP007 in Giguet-Covex et al. (2014), corresponding to primers Mamm02 in Taberlet et al. (2018)). To determine the diet composition, we used the universal primer pair Sper01_F & Sper01_R (Taberlet et al., 2018), which amplifies the P6-loop of the *trnL* intron of chloroplasts, a commonly-used meta-barcoding marker for plants (Valentini et al., 2009, Taberlet et al., 2012, Ibanez et al., 2013, De Barba et al., 2014). The Sper01 primers correspond to the g/h primers of Taberlet et al. (2007) that have been well-established for the study of large herbivore diets (Kartzinel et al., 2015, Nichols et al., 2016, Pansu et al., 2019).

All PCR were carried out in a final volume of 20 μL containing 2 μL of DNA extract. For the Sper01 primer pair, the amplification mixture consisted of 10 μL of AmpliTaq Gold® 360 master mix (Applied Biosystems), 0.5 μM of each primer and 0.16 μL (20 mg/mL) of bovine serum albumin (BSA, Roche Diagnostic). Polymerase activation was performed at 95 °C for 10 min, followed by 40 cycles of 95 °C for 30sec (denaturation), 50 °C for 30sec (primer annealing) and 72 °C for 60sec (extension) with a final elongation for seven minutes at 72 °C at the end. We carried-out three technical PCR replicates for Sper01 to reveal the diet. All experiments included extraction controls, blanks, PCR negative and positive controls. PCR products were purified using the MinElute PCR purification kit and sequenced on an Illumina HiSeq 2500 platform using a paired-end approach (2 × 125 bp). Sequence data were processed using OBITools software (Boyer et al., 2016) to (a) assemble and dereplicate reads, (b) match sequences to the original samples, (c) denoise the data by removing singletons, low-quality sequences, putative PCR/sequencing artefacts, and (d) taxonomically assign the remaining sequences. For taxonomic identification of sequences we built reference libraries for the local plant species by extracting the relevant parts of the EMBL (European Molecular Biology Laboratory) nucleotide database, the NCBI (National Center for Biotechnology Information) taxonomy, and a database for arcto-boreal plant species and bryophytes (Sønstebø et al., 2010, Willerslev et al., 2014, Soininen et al., 2015). Further cleaning and data analysis were done using R (R Core Team, 2017) and the final dataset was stored in a relational database using PostgreSQL (https://www.postgresql.org) to facilitate data analysis at the ecological level. For each DNA extract, we had three PCR replicates. To assess consistency across replicates, we calculated the distances of PCR replicates from their barycentres based on their sequence composition (PCR distances) and the distances between barycentres (sample distances). In consistent PCR reactions, PCR distances should be small (=zero under hypothetical perfect conditions with identical amplification across PCR replicates) compared to sample distances. We log-transformed sample distances to attain an approximately normal distribution and used the distance corresponding to the 5% percentile as a quality threshold for PCR replicates. We then removed all outlier PCR replicates with a distance larger than this threshold and also excluded sequences without a match to a reference sequence from further analyses. Annotated sequences were retained as molecular operational taxonomic units (MOTUs) and the number of reads for each MOTU were

Table 1
Results for the beta regression models showing the effect of deer density (Deer index) and food availability on the proportions of *Vaccinium* and pine in the spring diets of four deer species in Sweden. Analyses are based on the 2017 subset of the data, which included measurements for both food availability and deer density. The sample size (N) corresponds to the number of replicates (transects). Significant results are marked in bold.

Species	N	Response	Predictors							
			Deer index				Food availability			
			Estimate	SE	z	Pr (>|z|)	Estimate	SE	z	Pr (>|z|)
Moose	29	% Vaccinium	− 0.20	0.07	− 2.94	**0.003**	1.36	1.21	1.12	0.261
A. alces		% Pine	0.11	0.05	− 2.28	**0.023**	− 0.68	3.18	− 0.21	0.831
Roe deer	13	% Vaccinium	0.14	0.12	1.13	0.257	− 0.53	1.81	− 0.29	0.770
C. capreolus		% Pine	− 0.45	0.24	− 1.89	0.059	− 16.80	8.96	− 1.88	0.061
Red deer	20	% Vaccinium	0.02	0.11	0.16	0.873	1.34	1.62	0.82	0.410
C. elaphus		% Pine	0.06	0.12	0.50	0.617	− 8.28	5.97	− 1.39	0.165
Fallow deer	17	% Vaccinium	0.08	0.05	1.46	0.145	0.70	0.78	0.90	0.371
D. dama		% Pine	0.05	0.08	0.61	0.544	5.89	18.30	0.32	0.748

averaged across the remaining PCR for each sample. To confer the same weight to each fecal sample, we converted read abundances into relative read abundances (RRA), representing the proportion of each MOTU in each fecal sample. We removed MOTUs that did not represent at least 2.5% in at least one sample from the final dataset (Bison et al., 2015). RRA is increasingly used as a quantitative measure for the proportional composition of diets (Craine et al., 2015, Kartzinel et al., 2015, Deagle et al., 2019, Kowalczyk et al., 2019, Pansu et al., 2019, Churski et al., 2021), yielding similar conclusions to those derived from presence/absence data (Willerslev et al., 2014, Kartzinel et al., 2015, Kowalczyk et al., 2019). All quantitative results with respect to diet (e.g., diet composition, proportions of individual food items and references to consumption) in this study are based on RRA. Sequences could frequently only be assigned at genus level or above since the taxonomic resolution of the *trnL*-P6 plant barcode varies among plant families (Taberlet et al., 2007). We therefore summarized the proportions of all MOTUs corresponding to pine and *Vaccinium* (Table A1).

To account for the varying numbers of fecal samples found on different transects, we calculated average diets (RRA of pine and *Vaccinium*) for each deer species, year, month, and transect. The square transect (4 km) was thus our sampling unit for statistical analyses. The transect-scale diet data were then linked with the spring deer density index of the respective sampling years (2015–2017) and to food availability measurements (2017 only).

2.4. Deer density index

Pellet groups were counted annually from 2015 to 2017 during spring (Öster Malma: March-May, Nordmaling: April-June) on 16 evenly spaced sampling plots along the 1x1 km square transects (Fig. 1a). Since pellet groups were counted just after snow melt, before leafing-out of the field layer, possible bias resulting from vegetation cover hiding pellets of smaller species was minimal. The circular sampling plots consisted of 100 m^2 (r = 5.64 m) for counts of putative moose and red deer pellet groups and of 10 m^2 (r = 1.78 m, same centre point) for roe and fallow deer. From 2016 onwards, roe and fallow deer pellet groups were counted on 100 m^2 in the Nordmaling region. To be included in the count, the centre of a pellet group had to fall within the plot boundaries. A pellet group had to consist of at least 20 individual pellets for moose and red deer or of 10 pellets for roe and fallow deer. Because plots were not cleaned between annual surveys, we counted only pellet groups that had been deposited after the leaf-fall of the previous autumn; i.e., pellet groups that were deposited above the leaf litter and not heavily decomposed. Because we were interested in the effect of the smaller deer on moose, we combined the pellet counts of the three smaller deer species (red, fallow and roe deer) into one deer density index. Because moose pellets can be distinguished from smaller deer with high confidence (Spitzer et al., 2019), we did not expect the deer density index to be confounded with possibly misclassified moose pellet groups. Since

moose densities were similar across the study area, not adding moose pellet groups to the deer index did not bias the density gradient; i.e., adding moose pellets would have been similar to adding a constant. Levene's test showed no difference between the deer index and the deer index plus moose counts (F = 0.02, P = 0.88). The deer density index was standardized to a unit of pellet groups per 100 m^2. We excluded transects on which less than 75% of the total plot area had been surveyed from further analyses. We also removed one outlier transect with an extremely high deer density index (25.7 pellet groups per 100 m^2) that probably resulted from a recording error in the field.

2.5. Food availability

We measured variation in food availability alongside the bimonthly collections of fecal samples on the same subset of 33 transects. Following the step-point method (Evans and Love, 1957, Coulloudon et al., 1999), we recorded vegetation hits on a pole approximately every 40 m (=100 measurements per transect) along each 4 km transect within the browsing stratum of moose, i.e., between 0 and 3.0 m (Nichols et al. (2015), sensu Landman et al. (2013)) Such vegetation hits are analogous to bites that could be taken by a foraging moose and can easily be transformed to proportions. Because moose fed almost exclusively on woody vegetation (~90%, Fig. 1b) during the study period, we calculated food availability for pine and *Vaccinium* as a proportion of the total hits on woody vegetation.

2.6. Statistical analysis

The response variables in our study, i.e. the proportions of pine and *Vaccinium* in deer diets, represented continuous measurements which were bounded by 0 and 1. For such restricted data, linear regression models can result in misleading conclusions (Galvis et al., 2014), e.g., yield fitted values exceeding the confined domain (Ferrari and Cribari-Neto, 2004, Bonat et al., 2015). To test the effect of the predictors (deer density and food availability), we therefore used beta regression models (Ferrari and Cribari-Neto, 2004) as implemented in the R package 'betareg' (Cribari-Neto and Zeileis, 2010) using the logit-link option. Beta regression has become a well-established approach for modelling variables which assume values in the standard interval (0,1) such as rates or proportions (Kelley et al., 2007, Wallis et al., 2009, Bayes et al., 2012, Yellareddygari et al., 2016). Because the *betareg* function cannot process zeros, we added 1×10^{-5} to the proportions of all diet items. For our analyses, we combined the data from both study regions (Öster Malma and Nordmaling) because they represented a strong gradient in the density of the smaller deer species but not moose. We analysed each of the three collection years (2015–2017) separately to asses if the feeding pattern of pine and *Vaccinium* remained consistent. The effect of food availability on the proportion of pine and *Vaccinium* in deer diets could only be tested on the 2017 subset of the diet data as food
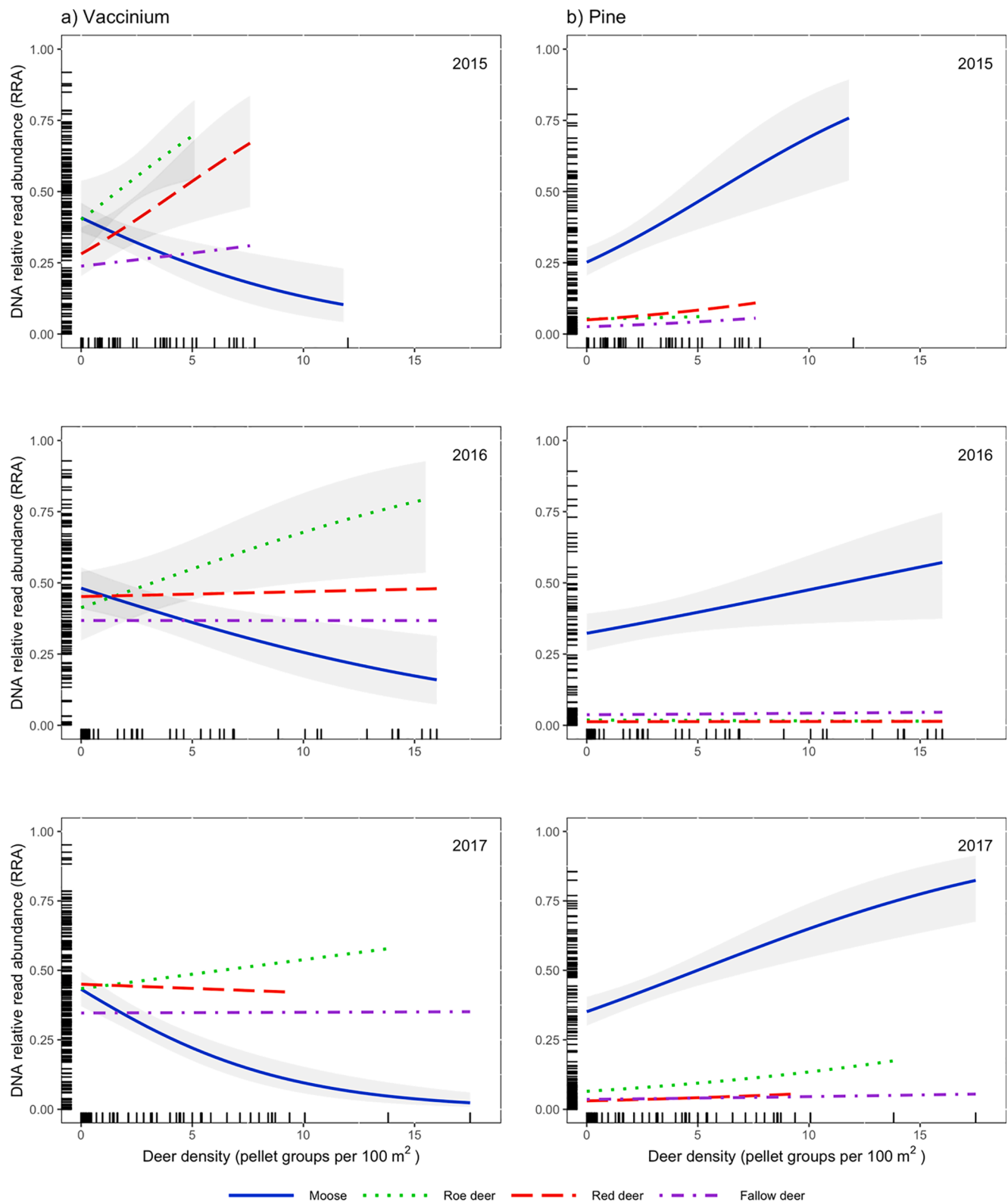
Fig. 2. Beta regressions showing the relationship between deer density and the proportion of *Vaccinium* (a) and pine (b) in the spring diets of four deer species in Sweden (moose *Alces alces*: solid blue line, roe deer *Capreolus capreolus*: dotted green line, red deer *Cervus elaphus*: dashed red line, fallow deer *Dama dama*: point-dashed purple line) across three years (2015–2017). The results in (a) and (b) refer to the same fecal samples and have been plotted separately solely for better visibility. Confidence intervals (95% CI) are indicated in grey and only shown for significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Results for the beta regression models showing the effect of deer density on the proportions of *Vaccinium* and pine (response) in the spring diets of four deer species in Sweden across three years. The sample size (N) corresponds to the number of replicates (transects). Significant results are marked in bold.

Species	Year	N	Response	Estimate	SE	z	Pr (>|z|)
Moose	2015	92	% Vaccinium	− 0.15	0.04	− 3.41	**< 0.001**
A. alces			% Pine	0.19	0.05	4.01	**< 0.001**
	2016	57	% Vaccinium	− 0.10	0.03	− 3.17	**0.002**
			% Pine	0.06	0.03	2.20	**0.028**
	2017	87	% Vaccinium	− 0.20	0.03	− 6.18	**< 0.001**
			% Pine	0.12	0.03	4.57	**< 0.001**
Roe deer	2015	22	% Vaccinium	0.24	0.10	2.37	**0.018**
C. capreolus			% Pine	0.03	0.13	0.24	0.807
	2016	16	% Vaccinium	0.11	0.05	3.32	**0.021**
			% Pine	− 0.02	0.05	− 0.31	0.756
	2017	39	% Vaccinium	0.04	0.04	1.10	0.275
			% Pine	0.08	0.05	1.75	0.081
Red deer	2015	41	% Vaccinium	0.21	0.08	2.88	**0.004**
C. elaphus			% Pine	0.11	0.07	1.59	0.111
	2016	36	% Vaccinium	0.01	0.03	0.25	0.802
			% Pine	0.006	0.03	0.22	0.829
	2017	55	% Vaccinium	− 0.01	0.05	− 0.27	0.786
			% Pine	0.07	0.05	1.42	0.157
Fallow deer	2015	27	% Vaccinium	0.05	0.07	0.71	0.480
D. dama			% Pine	0.11	0.06	1.72	0.086
	2016	29	% Vaccinium	−0.00008	0.02	− 0.003	0.998
			% Pine	0.01	0.04	0.39	0.695
	2017	46	% Vaccinium	0.001	0.04	0.03	0.973
			% Pine	0.03	0.04	0.70	0.481

availability was measured only during that year.

To assess whether the proportions of pine and *Vaccinium* in deer diets differed throughout the year under conditions of different deer densities, we assigned transects to two deer density classes ("high" ≥ 3rd quartile of the deer density index, and "medium–low" for all below this threshold). We then averaged deer diets for each density class at a monthly resolution and added locally fitted smoothing curves (function *loess* in R) to these data. All statistical tests were carried out in R (R Core Team, 2017) at a significance level of alpha = 0.05.

3. Results

The field collections yielded 2177 fecal samples from the four deer species. Of those, a total of 1724 (79%) passed the DNA quality filtering criteria (moose [8 0 8], roe deer [1 9 5], red deer [3 8 9], and fallow deer [3 3 2]). A total of 111 (88%) transects yielded both diet data and passed the quality criteria for the pellet group counts. At the ungulate community level, *Vaccinium* comprised the largest proportion (42%) in deer spring diets (Fig. 1b) compared to other woody (20%, except pine) or herbaceous food items (21%, graminoids and forbs). At the deer species level and apart from *Vaccinium*, moose consumed largely pine (38%), whereas the three smaller deer species fed mostly on herbaceous vegetation (roe deer: 22%, red deer: 23%, and fallow deer: 38%, Fig. 1b).

The deer density index ranged from 0 to 17.50 pellet groups per 100 m^2 ($\overline{x}$ = 2.18, SD = 3.61). Availability of pine and *Vaccinium* had no significant effect on the proportion of these food items in the diet of any of the four deer species for the 2017 spring data (Table 1). Deer density significantly affected moose diet. The proportion of pine in moose diet increased with increasing deer density whereas the proportion of *Vaccinium* decreased. The same pattern was consistently observed across the three years (2015–2017; Fig. 2 & Table 2).

The diets of the smaller deer species were either unaffected by deer density or, for *Vaccinium*, showed the opposite pattern to moose, i.e., the proportion of *Vaccinium* in diets increased with increasing deer density (2015: roe deer and red deer, 2016: roe deer; Fig. 2).

The feeding patterns of moose on pine and *Vaccinium* varied across the year in similar ways in areas of high and low deer density but, consistent with the spring observations, moose diets consistently contained more pine and less *Vaccinium* in areas with high deer density (Fig. 3). Moreover, in areas of high deer density, the proportion of

Vaccinium in moose diet was highest in autumn when the proportions of *Vaccinium* in the diets of the smaller deer were lowest. Throughout the year, proportions of *Vaccinium* in moose diet remained relatively constant whereas the smaller deer showed more seasonal patterns with *Vaccinium* utilization being high during spring and winter and lower during summer and autumn.

4. Discussion

With increasing deer density, moose diets contained less *Vaccinium* and higher proportions of pine. In contrast, the diets of the smaller deer species contained very little pine and the proportion of *Vaccinium* in their diets remained the same or increased with increasing deer density. These results support our hypothesis that feeding competition from smaller deer might be driving moose towards increasing their consumption of pine. Although variation in the availability of these forage items did not explain any of these trends, it is important to remember that we measured availability of these two food resources as proportions of available bites and did not quantify the absolute size or mass of these bites. We suggest that the possible feeding competition between moose and smaller deer may be caused by a change in average bite size of *Vaccinium*. Under conditions of high browsing pressure, it is reasonable to expect dwarf shrubs to be short and stunted. Unfortunately, we did not measure the height of the field layer during our original diet study but personal observations and comments from field personnel support these suppositions. In addition, recently collected data on the height of *Vaccinium* shrubs in forest stands within our study area showed a clear negative relationship between shrub height and deer density (Fig. A1), providing further evidence that browsing by smaller deer may strongly reduce shrub height, and thus maximum available bite size to moose. Similar effects of deer on the field layer have been shown, for example, for white-tailed deer in North America (Rossell et al., 2005, Rooney, 2009) and red deer in Norway, (Hegland et al., 2005, Melis et al., 2006, Speed et al., 2014). Shorter *Vaccinium* shrubs offer smaller bites, thereby reducing foraging efficiency for large browsers like moose. To compensate, moose may then be prompted to switch to higher foraging strata, which concurs with our observation of a higher proportion of pine in moose fecal samples in areas with high deer density.

The choice of pine as an alternative bulk food to *Vaccinium* is also consistent with the bite size hypothesis as bites of pine have been found
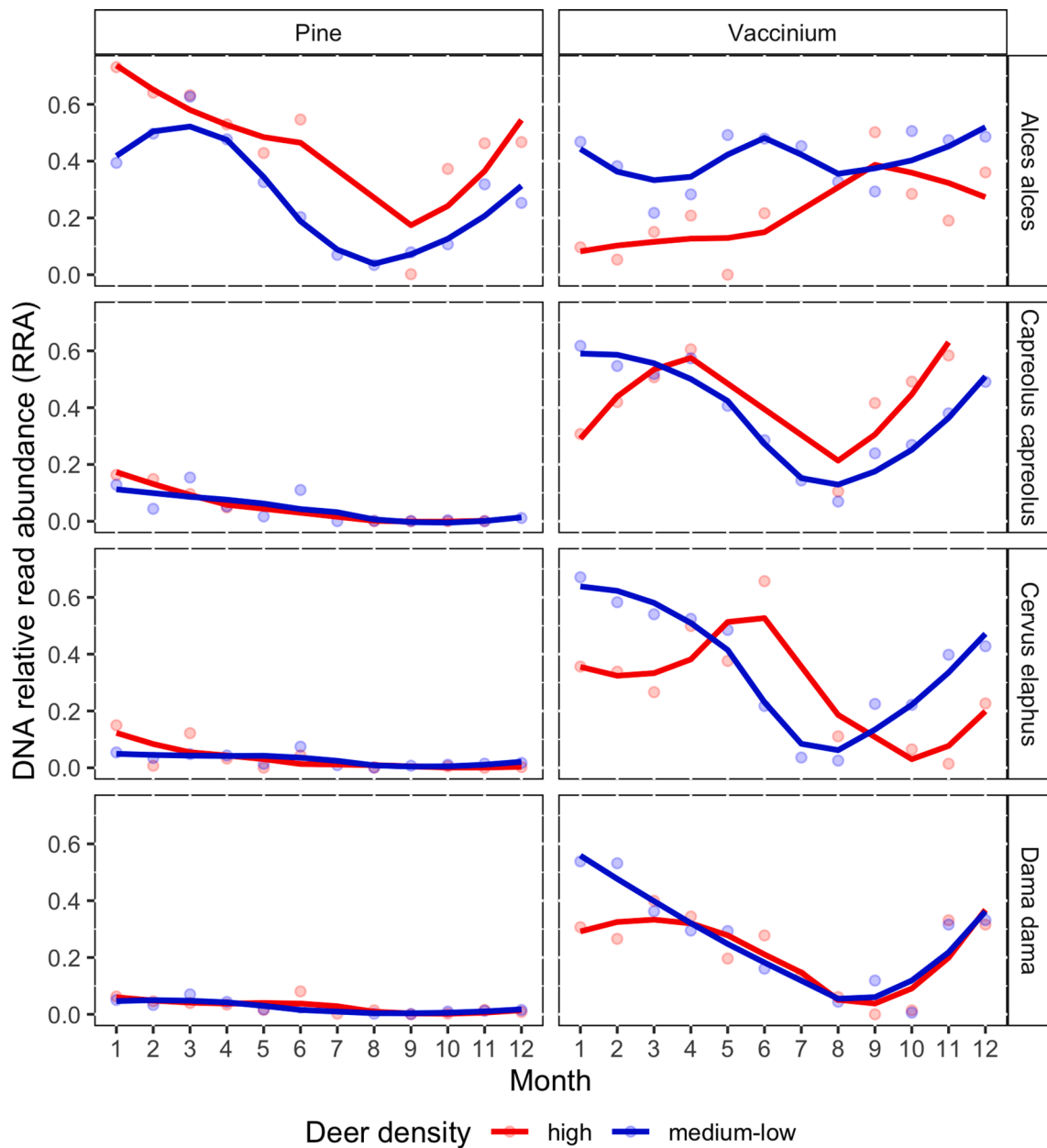
Fig. 3. Average proportions of pine and *Vaccinium* in the diet of four deer species in Sweden (moose *Alces alces*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, and fallow deer *Dama dama*) across the year in areas of different deer density; high (red) and medium–low (blue). Smoothing curves were fitted with function *loess* in R. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to contain more biomass than those on deciduous species (Hagen, 1958, Cederlund et al., 1980). The only other abundantly available tree forage in our study area were Norway spruce, which is usually avoided by moose and birch that ranks similarly to Scots pine in moose preference (Shipley et al., 1998).

The consumption of *Vaccinium* by the smaller deer species (i.e., the proportion of *Vaccinium* DNA reads in their feces) was not negatively affected by deer density. In some instances, we even found the opposite pattern; i.e., increases of *Vaccinium* in deer diets with increasing deer densities (roe deer 2015 and 2016 and to a lesser degree also red deer; Fig. 2). These findings might be explained by the circumstance that under conditions of high deer density, alternative food items such as the

first spring forbs and graminoids quickly become depleted and the deer species continue browsing on *Vaccinium* instead. Small browsers like roe deer (Hofmann, 1989) in particular, would likely respond to such conditions by seeking out the best bites of regenerative growth on dwarf shrubs. Moreover, the threshold for shrub size that still allows efficient browsing by smaller deer species is likely to be lower than for moose, which lends further support to the bite size hypothesis as the driver behind the change in moose browsing behaviour.

Further study is needed to determine whether changes in the height (and correspondingly average bite size) of *Vaccinium* along the deer density gradient in our study area explain the observed changes in moose diet and if such changes in the availability of edible biomass are

causally linked to deer browsing or other factors such as differences in the light regime or soil properties, particularly with regard to forest management practices. Because browsing damage has been shown to increase the accumulation of secondary metabolites in bilberry (Persson et al., 2012), it would also be worth investigating if such changes to the chemical and nutritional properties of *Vaccinium* affect subsequent browsing by deer.

Classically, studies of moose browsing have focused on trees and identified diameters at which shoots and stems are typically bitten (Edenius, 1991, Jia et al., 1997, Nichols et al., 2015). Future research should address whether bite size or shrub height thresholds exist for moose (and other deer) foraging on dwarf shrubs. Such thresholds would likely be determined by the overall dry matter intake offered per bite rather than shoot diameter.

Bilberry produces new shoots every year and is, to some extent, able to recover from herbivory by mobilizing the large nutrient reserves stored in its underground parts for regenerative growth (Tolvanen et al., 1994). The annual consumption patterns of *Vaccinium* for the smaller deer suggest that they might take advantage of the fresh shoots in late spring and then switch to other foods, presumably the emerging forbs and grasses, during the summer so that *Vaccinium* browsing by smaller deer reaches its low around August. Interestingly, during this same period, moose browsing on *Vaccinium* peaked in areas with high deer density (Fig. 3), with moose possibly taking advantage of regenerative growth. Such temporal resource partitioning provides further evidence for the possible feeding competition between moose and smaller deer over dwarf shrubs.

In summary, we conclude that there is support for our hypothesis that smaller deer push moose towards eating more pine along a gradient of deer density. We suggest that this is likely driven by moose seeking larger bites in higher strata once forage at lower levels has been depleted as is predicted by the bite size hypothesis. These findings strengthen the suggestion first reported from African systems, that small browsers might displace large ones from shared resources at lower foraging strata by transforming vegetation to a state below the thresholds imposed by bite size and intake rate on large browsers (Woolnough and du Toit, 2001). Such changes in resource use by one species in the presence of others also points toward the potential for interspecific competition. The fact that moose included a higher proportion of *Vaccinium* in their diet in the absence of smaller deer, suggests that they prefer *Vaccinium* over pine. Indication of this was found in a recent study showing that in areas of southern Sweden, where moose diets are heavily dominated by conifers (predominantly pine), mean population calf body mass is relatively low (Felton et al., 2020). To determine if reduced access to *Vaccinium* may negatively affect moose fitness, further research should focus on the nutritional values of pine and *Vaccinium* and relate their use to indices of moose performance. In North America, Schrempp et al. (2019) found that moose population trends in Idaho fluctuated with changes in the availability of moderate-energy forage shrubs.

5. Implications for forest management

The increased use of pine by moose with increasing deer density may have ramifications for forestry if this behaviour leads to higher levels of browsing damage to commercial stands. Assuring optimal growing conditions and a rich supply of *Vaccinium* in the forest field layer may alleviate the browsing pressure by moose on pine and also appears to be a crucial component for the maintenance of flourishing multispecies ungulate communities. Thus, the small shrubs in the field layer of Sweden's boreal forest might indeed be of large importance as an irreplaceable strand in northern food webs that even directs the largest browser. In the mitigation of the forestry-moose conflict over pine, managing key food items like *Vaccinium* and the populations of smaller deer might be of equal or even greater importance than simply controlling the number of moose. Maintaining a flourishing field layer may also play an important role for managing healthy moose populations. If the dwarf shrubs are an important resource, and small deer outcompete moose over this resource, forest management that promotes dwarf shrubs will also alleviate these competitive effects (Schrempp et al., 2019).

CRediT authorship contribution statement

Robert Spitzer: Conceptualization, Methodology, Resources, Formal analysis, Investigation, Visualization, Writing - original draft, Writing - review & editing. **Eric Coissac:** Data curation, Software. **Annika Felton:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Funding acquisition. **Christian Fohringer:** Visualization, Writing - original draft. **Laura Juvany:** Resources. **Marietjie Landman:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Navinder J. Singh:** Conceptualization, Methodology, Writing - original draft. **Pierre Taberlet:** Investigation, Writing - original draft, Writing - review & editing, Supervision. **Fredrik Widemo:** Conceptualization, Methodology, Writing - original draft. **Joris P.G.M. Cromsigt:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The author declare that there is no conflict of interest.

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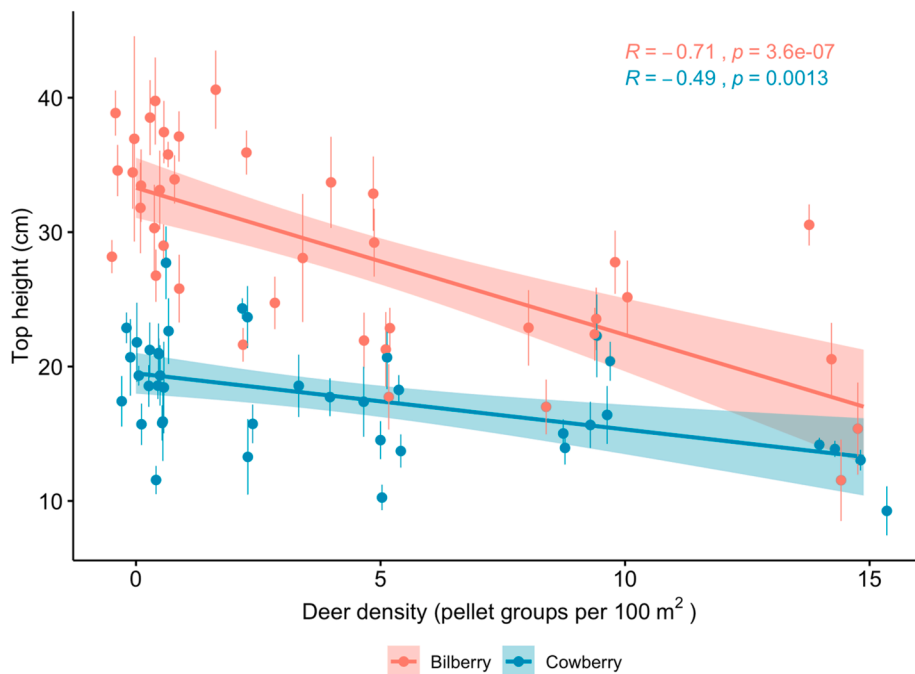## Appendix A

See Fig. A1 and Table A1.

Fig. A1. Negative relationship between deer density and shrub height for the two most common *Vaccinium* species in Sweden (bilberry *Vaccinium myrtillus* [red] and cowberry *Vaccinium vitis-idaea* [turquoise]). Each dot represents a circular sampling plot (N = 40, r = 10 m) within ten production forest stands in each of the northern and southern study areas. The heights of five individual plants of each species were measured per plot in spring 2020. Forest stands were 45–70 years old and dominated by Scots pine *Pinus sylvestris*. Shown are the mean values with error bars indicating the standard error. Regression lines are shown with 95% CI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table A1

Food items and corresponding MOTUs in spring diets of four deer species in Sweden. The quantities correspond to the mean proportions in diets (DNA relative read abundance, RRA) and their standard deviations (SD). The MOTU *Vaccinium* encompasses sequences that match several *Vaccinium* species including bilberry *Vaccinium myrtillus*, which could only be assigned at genus level.

Food item	MOTUs	Moose *A. alces* N = 808 RRA (SD)	Roe deer *C. capreolus* N = 195 RRA (SD)	Red deer *C. elaphus* N = 389 RRA (SD)	Fallow deer *D. dama* N = 332 RRA (SD)
Pine	*Pinus*	0.40 (0.27)	0.06 (0.10)	0.03 (0.07)	0.04 (0.06)
	Pinus contorta	< 0.01	< 0.01	< 0.01	< 0.01
Vaccinium spp.	*Vaccinium*	0.23 (0.18)	0.28 (0.14)	0.15 (0.13)	0.17 (0.15)
	Vaccinium microcarpum	< 0.01	< 0.01	< 0.01	< 0.01
	Vaccinium ovalifolium	0.13 (0.10)	0.15 (0.08)	0.08 (0.07)	0.10 (0.08)
	Vaccinium oxycoccos	< 0.01	0.01 (0.04)	< 0.01	0.01 (0.03)
	Vaccinium uliginosum	< 0.01	< 0.01	< 0.01	< 0.01
	Vaccinium vitis-idaea	0.01 (0.03)	0.07 (0.10)	0.24 (0.23)	0.06 (0.09)

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